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Biogeography of ecuadorian grasses

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Introduction

Even from simple fieldwork experience it is very obvious that subfamilies and tribes of Ecuadorian grasses have different and rather distinct altitudinal distribution. Pooideae are almost exclusively in the highlands above 2000 m and Panicoideae are predominantly in the lowlands below 2000 m while other subfamilies have more scattered altitudinal distribution but whole subfamilies or tribes often have other specific ecological preferences.

Material and methods

The base of the present work is information in a checklist of vascular plants of Ecuador by Jørgensen & Leon (1999). In this are recorded a total of 138 genera and 557 species of grasses in Ecuador. Of these many have actively been introduced from the Old World for cultivation. Some of these have very aggressively spread outside the cultivated fields and have become naturalized and often a severe menace to local grass species and many other herbs. Many other species have been introduced accidentally, some of these are spreading and more or less naturalized while others are more restricted and have only been recorded one or few times.

By exclusion of introduced species and species only occurring in the Galapagos Islands there are 102 genera and 429 species that are native to the Ecuadorian mainland. Of these species 55 are recorded as endemic to Ecuador which means that among native species there are 12.8% endemics.

For each species in the checklist the altitudinal range is given based on vouchers in herbaria. The altitudes are recorded as intervals of 500 m up to >4500 m. The present diagrams were constructed on base of this. If a single interval is lacking it is filled in. A few additions of intervals have been made, based on later records and also a few obvious errors have been

corrected. A few species with a note of "reports not confirmed" have been excluded. The taxonomy and nomenclature of subfamilies, tribes, and genera generally follow Clayton & Renoize, 1986.

Palaeogeography and Paleoecology

The Cordilleras de los Andes are relatively very young mountains that are still geologically very active with tectonics and vulcanism. According to van der Hammen (1979), the open páramo region above the natural forest line was only created about 3 million years ago in Colombia. It is here presumed that the age is about the same in Ecuador. It is also presumed that the present natural forest line in Ecuador is about or above 4000 m and that most or all grass dominated páramos below that altitude are antropogenic, i.e., created and maintained by human activity during the last few thousands years (Lægaard, 1992). Such newly created open biotopes have probably been invaded by species belonging to the superpáramo, i.e., the vegetation above the natural forest line. The Amazonian rain forest is much older than the high mountain range though there have been many variations in the extent of the densely forested area, especially through the Pleistocene glacial periods.

The coastal area is here presumed to have been rather dry or at least seasonally dry because of the relatively cold sea currents. The landscape between the dry coastal zone and the rain forest may have been low and flat or with low mountains but there must clearly have been a warm tropical climate with variable humidity.

Biotopes for grasses are extremely variable but the great majority of species are more or less light demanding and only a few tolerate the full shade of a forest bottom. Many species are pioneers in disturbed grounds.

Subfam. Bambusoideae — Fig. 1.

"Herbaceous Bamboos"

The group is heterogeneous and divided in several tribes but evolutionary it is considered to be very old and close to the roots of the grass family. There is a diversity center for the herbaceous bamboos in tropical America with a few genera also in the Old World. Ecologically they all belong to the tropical rain forest and have probably been there throughout the Tertiary. At present they are mostly confined to the tropical lowland, only a few are found in forests up to 1500 m. They are very specialized, some tolerate a slight disturbance of the forest but disappear immediately on clearance of the forest.

Bambuseae

The tribe is morphologically very specialized in relation to other grasses, including the herbaceous bamboo's. The diversity center for the tribe is in tropical Asia. In our area there are rather few species in the tropical lowland, mainly ***Guadua***. Most genera and species of the real bamboo's belong to mountain forests and several species of ***Chusquea*** and the specialized genus ***Neurolepis*** reach the páramo region. Most of the genera are endemics to the Andean region from Patagonia to Central America. Many species are endemic to rather small areas, e.g., in ***Neurolepis*** with 12 species in Ecuador of which six are endemic. *Chusquea* is recorded with 17 species and five endemics but according to L.G. Clark (pers. com.) there

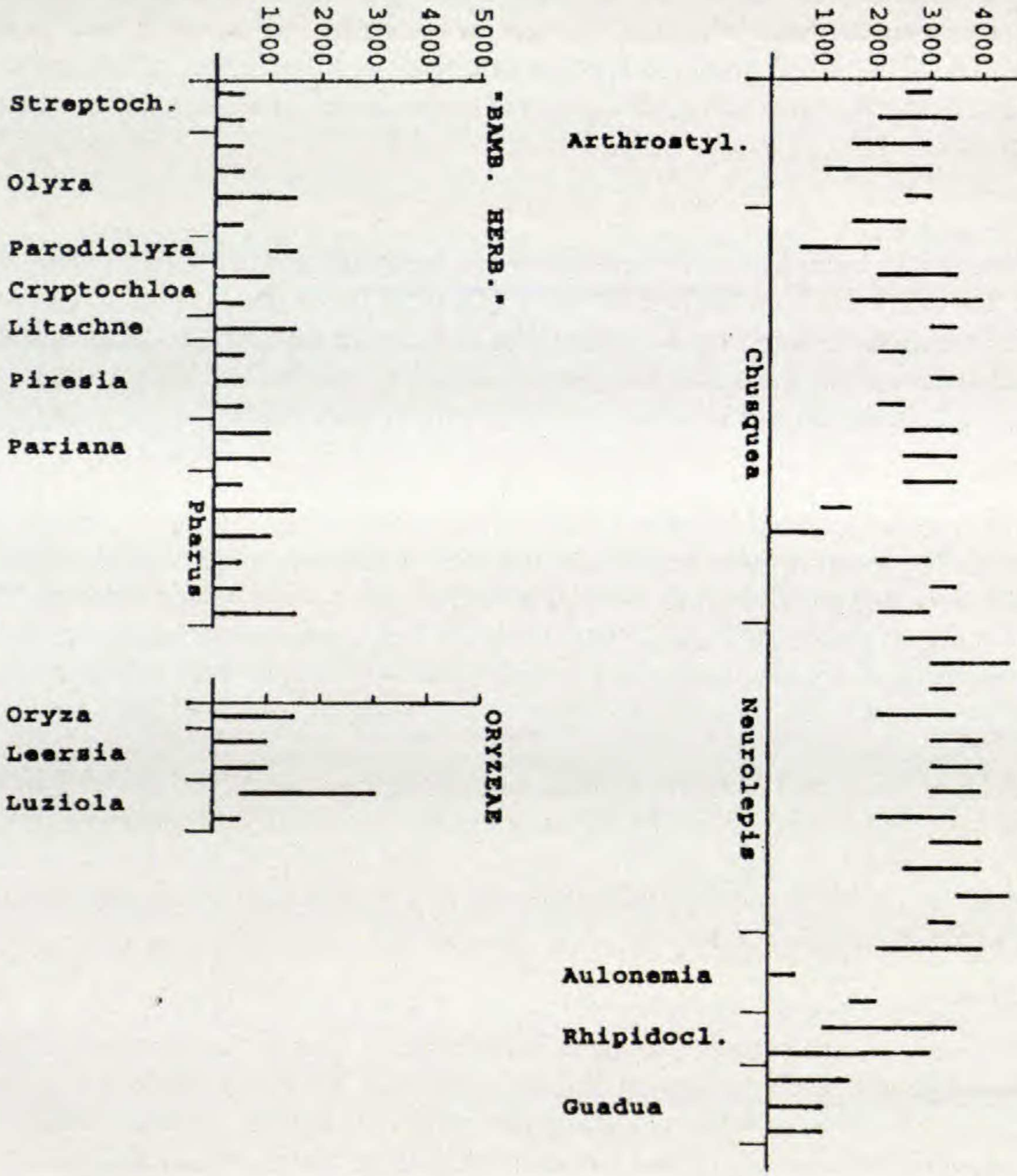

Figure 1. Altitudinal distribution of all native Ecuadorian Bambusoideae (Bambuseae, "Herbaceous bamboos", and Oryzeae). The genera are in order from Clayton & Renvoize, 1986, and the species are in alphabetic order following Jørgensen & Leon, 1999. Each bar represents a species.

are about 10 more species still undescribed and these are probably all endemics.

The present distribution suggests that the evolutionary base of the group belonged to the tertiary forests and that during the uplift of the mountains there was a rapid evolution resulting in a great number of species.

Oryzeae

A small group that is sometimes treated as a tribe under Bambusoideae and sometimes as an independent subfamily. Most of the species belong to swamps or at least to moist biotopes. The altitudinal distribution is rather scattered. Representatives of the group may easily have been in the area before the uplift and some species have been able to adapt to a colder climate.

Subfam. Pooideae — Fig. 2.

Nearly all genera and native species of this subfamily are confined to areas above 2000 m and many reach the highest altitudes with plant life at about 5000 m. Before the uplift of the mountains there would not have been biotopes for any representatives and all are supposed to have immigrated after the general uplift, i.e., within about three million years. Many species are endemic to Ecuador or at least to the Central Andes.

Stipeae

All species are found in open conditions and mostly in dry biotopes, often in light, sandy soils. The genus ***Stipa*** is worldwide, the other genera are only in the Americas and especially ***Aciachne*** and ***Ortachne*** are high mountain plants of the Andes. Miocene fossils are known from southeastern United States (Clayton & Renvoize, 1986) and progenitors of the Andean genera may have migrated from there during the uplift of the mountains

Poeae

All five genera and 28 native species are from regions above 2000 m and most from above 3000 m. The two largest genera, ***Festuca*** and *Poa*, have both several endemic species, probably as a result of splitting during migration and adaptation to extreme altitudes. ***Puccinellia*** has only been recorded at one site, in a very small area of saline springs and with salt extraction in central Ecuador.

Aveneae

The same general pattern is found as in Poeae. Most species occur between 2500 and 4500 m and several reach the highest altitudes with plant life while only a few are found below 2000. One of these, ***Polypogon elongatus***, is the only species of the subfamily that is commonly found in tropical lowland (not registered below 500 m but certainly occurring). The largest genus, ***Calamagrostis***, has 27 species, nine of these are endemics. The representatives seem to more close to species in the southernmost parts of South America and the genus has probably migrated from there after creation of the Andean zone above the forest line.

The three small tribes, **Meliceae**, **Bromeae**, and **Triticeae**, have distribution patterns almost as the rest of the subfamily.

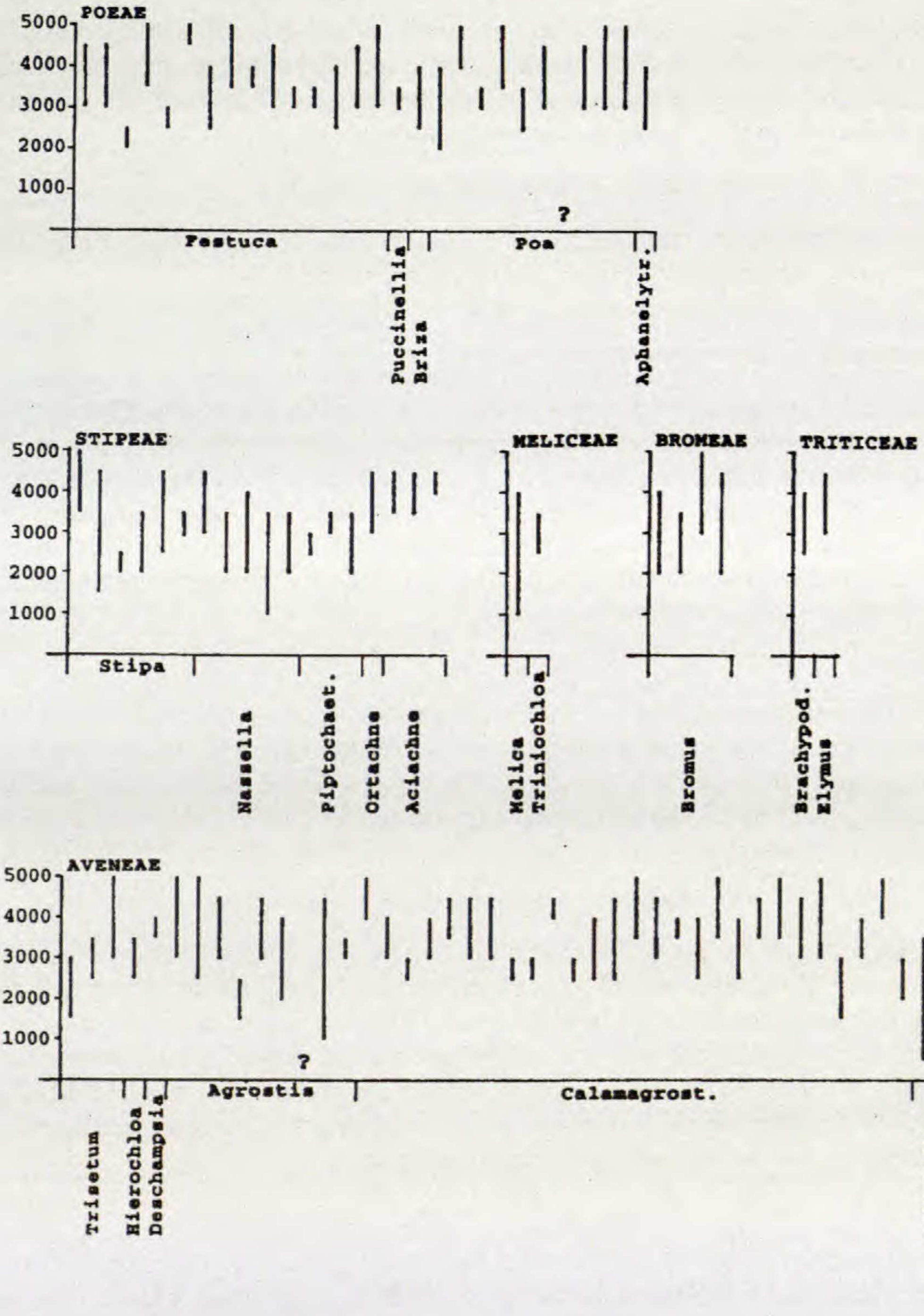

Figure 2. Altitudinal distribution of all native Ecuadorian Pooideae (Poeae, Stipeae, Meliceae, Bromeae, Triticeae, and Aveneae). Further explanation under Fig. 1.

Subfam. Centothecoideae — Fig. 3.

A small and probably primitive subfamily of nearly entirely tropical distribution in both Old and New World. Nearly all are forest grasses.

Centotheceae

Orthoclada has another species in Tropical Africa, ***Zeugites*** is only in tropical America. Both follow the patterns of some of the Bambusoideae and may easily have been in Ecuador long before the uplift of the mountains. ***Orthoclada*** has remained a tropical rain forest grass while ***Zeugites*** has adapted to the cooler mountain forests.

Subfam. Arundinoideae — Fig. 3.

The subfamily has two tribes that are very different and often separated with Aristideae treated as a distinct subfamily or included in, e.g., Chloridoideae.

Arundineae

The tribe is mainly Southern Hemispheric with a number of genera in South America, South Africa, and Australia and rather few genera extending into the Northern Hemisphere. ***Gynerium*** is a tropical forest plant (swamps, riversides) and probably of old origin in the region. ***Cortaderia*** is an amphi-pacific genus and in Ecuador clearly a páramo species (below 3500-4000 m it only occurs in disturbed sites) which must have arrived at a late stage of the uplift of the mountains. ***Phragmites*** is rare in Ecuador and has an interesting distribution as it occurs in the coastal lowland and in swamps at mid-altitude but hardly in the intervals between. The species may consist of two ecotypes.

Aristideae

Only one species is common and widely distributed, ***Aristida adscensionis***, all others are scattered to rare. All are confined to light open and dry to extremely dry biotopes but the altitudinal ranges of the species are rather scattered. It is suggested that the genus and some of the species may easily have been present in the dry or semidry coastal zone or low mountains before the uplift of the Andes.

Subfam. Chloridoideae — Fig. 3.

It is characteristic for the whole subfamily that the species are light demanding but seem to be more or less independent of temperature and thus of altitude and occur with more or less equal representation from sea level to about 3500 m. It is also characteristic that the subfamily has many genera with only one or very few species and in Ecuador there are only two with about 10 species. Of the 20 Ecuadorian genera about 13-14 are exclusively or predominantly in the New World. Many species are weedy but most of these are introduced from the Old World and are not included in the present study.

Eragrosteae

The altitudinal distribution is very varied with many species occurring above 3000 m. All the species are in full light, often on rocky outcrops, in degraded land or similar biotopes. Most are perennial and found in more or less stable vegetation.

It is supposed that many may have been present under similar conditions in the area

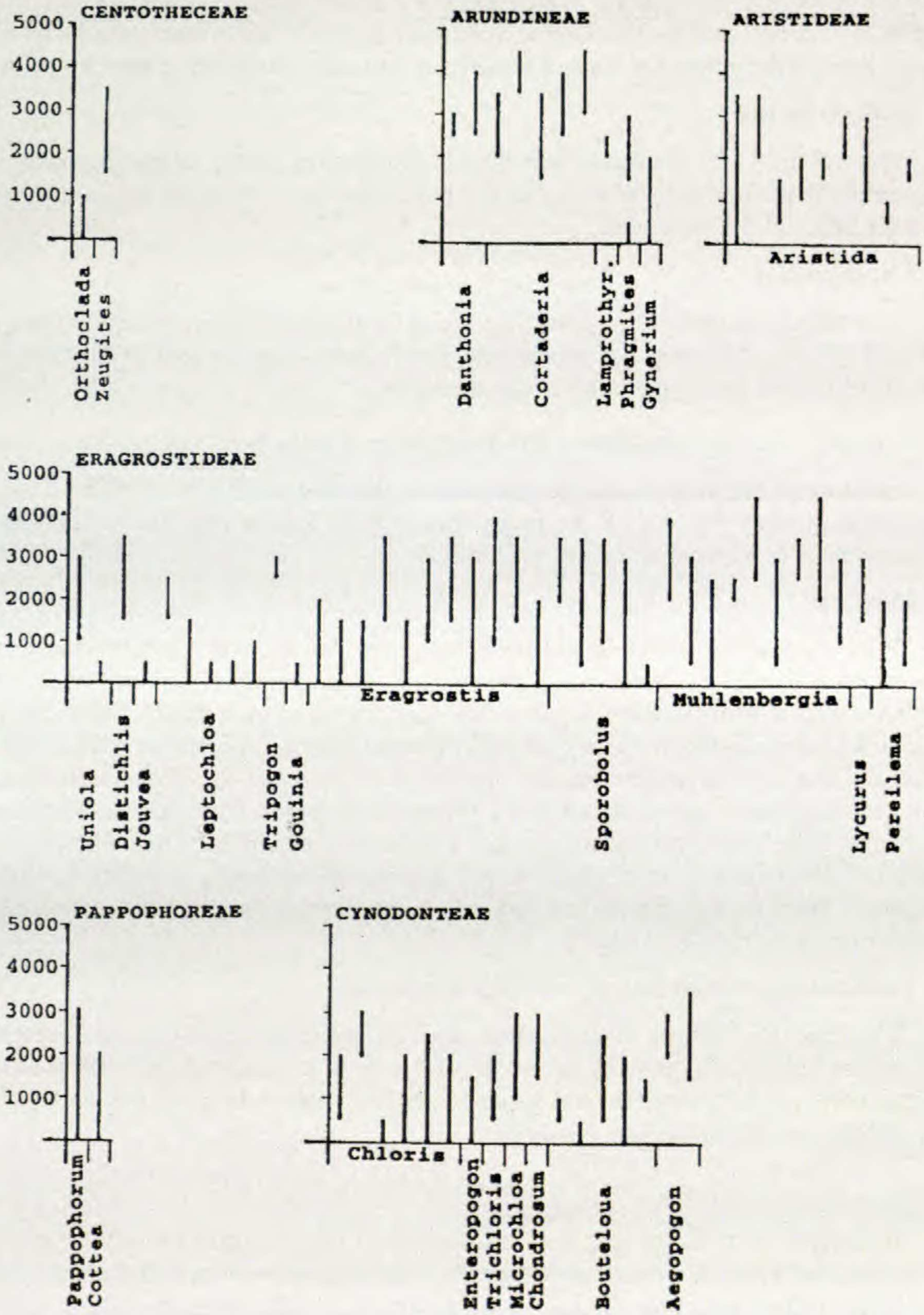

Figure 3. Altitudinal distribution of all native Ecuadorian Centothecoideae (Centotheceae), Arundinoideae (Arundineae and Aristideae), and Chloridoideae (Eragrostideae, Pappophoreae, and Cynodonteae). Further explanation under Fig. 1.

before the uplift of the mountains. ***Muhlenbergia*** is a very variable genus. It has a diversity center in Mexico and southeastern United States and there has clearly been introduced several different lines of the genus and each of these have had a development in the Central Andes.

Pappophoreae

A small tribe with Southern Hemispheric distribution, nearly all species occur in dry to extremely dry biotypes. They may easily have been present in the dry coastal region before the uplift of the mountains.

Cynodonteae

The altitudinal distribution resembles that of Eragrostideae but generally the species are found at lower altitudes. All genera may easily have been present in the dry coastal lowland before and during the uplift of the mountains.

Subfam. Panicoideae — Fig. 4, 5.

Because of the unique spikelet structures in the subfamily it is considered the most recent evolutionary branch of the grass family and within the subfamily the tribe Andropogoneae is considered the most advanced.

Paniceae

Predominantly tropical lowland plants but many also occur at mid altitudes and a few reach the páramo regions. Some are extremely light demanding, others are shade tolerant and often occur at forest borders but none are real primary forest plants. Some are in dry biotopes but rarely in extremely dry, others are swamp plants. All genera may easily have been in the transition zone between the dry coastal region and the closed tropical forest. Several shade tolerant genera as ***Lasiacis, Pseudechinolaena, Oplismenus, Panicum*** sp. sp., etc. may have been in secondary biotopes as riversides etc. in the primary forest. During the uplift of the mountains many genera were able to follow with adaptation and evolution of new species. There are very few narrow endemics in the tribe but many species in the highlands are endemics to the Central Andes.

Isachneae, Arundinellaeae, and **Andropogoneae**

The altitudinal ranges in these tribes are even more scattered than in Paniceae but nearly all are light demanding. All genera may have been in the area before the uplift of the mountains and as in Paniceae several species have been able to adapt to the cooler climate but remained dependent on open conditions.

Conclusions

It is clear from the present material that most of the larger taxonomic groups as subfamilies and tribes of grasses are adapted to the same overall climatic conditions and major ecological traits as light demand or shade tolerance. This seems to indicate that such major climatic and ecological adaptations are of very old origin and have been kept in the subfamilies and tribes as conservative characters.

It is suggested as a hypothesis that deductions about the history and migration of the grasses in Ecuador can be drawn from their present altitudinal distribution and a general

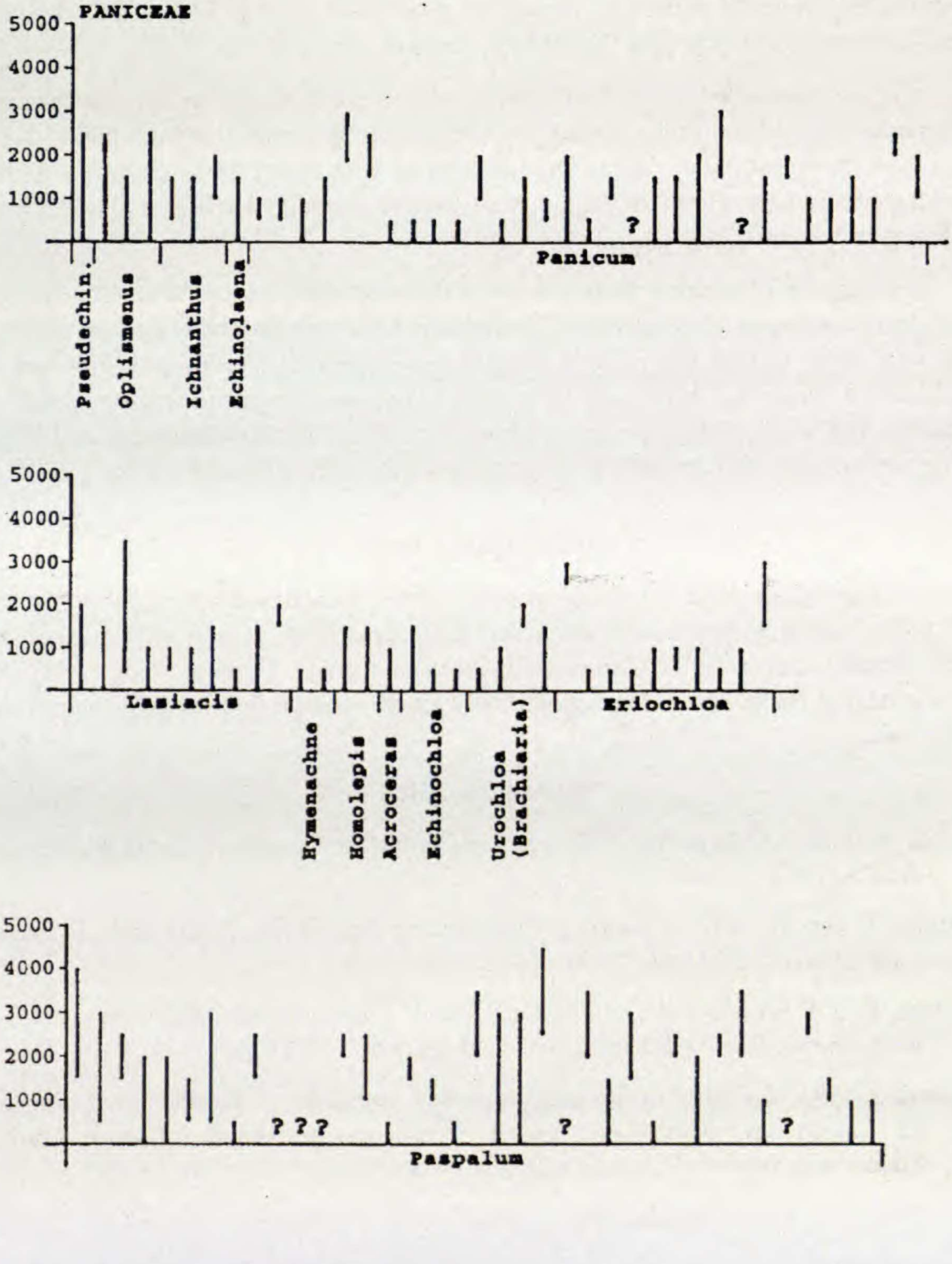

Fig. 4. Altitudinal distribution of all native Ecuadorian Panicoideae (Paniceae p.p.). Further explanation under Fig. 1.

knowledge about their ecology and geographical distribution.

Based on this, it is suggested that Bambusoideae, Centothecoideae, and a few Paniceae may have been in the area as forest grasses before the uplift of the mountains and that the changing environmental conditions during the process of uplift provoked an evolution of several new species in mountain forests and páramos.

It is suggested that most of the Chloridoideae, Aristideae, Andropogoneae, and many Paniceae may have been in the area in the tropical dry or semidry coastal region and the transition to the forest region. Many have remained in the same type of environment while others have followed the uplift of the mountains and have adapted to higher altitudes but are still living in open biotopes.

It is suggested that all Pooideae, most of Arundineae, and probably some Chloridoideae, especially of the genera ***Muhlenbergia, Sporobolus*** and ***Eragrostis*** have immigrated during the uplift of the mountains and filled in vacant niches especially after the new biotopes were created above the natural forest line. Most probably some immigrated from the south, e.g., ***Calamagrostis,*** while others immigrated from the north, e.g., ***Muhlenbergia*** and Stipeae. During the immigration there was in many genera a rapid evolution of new species.

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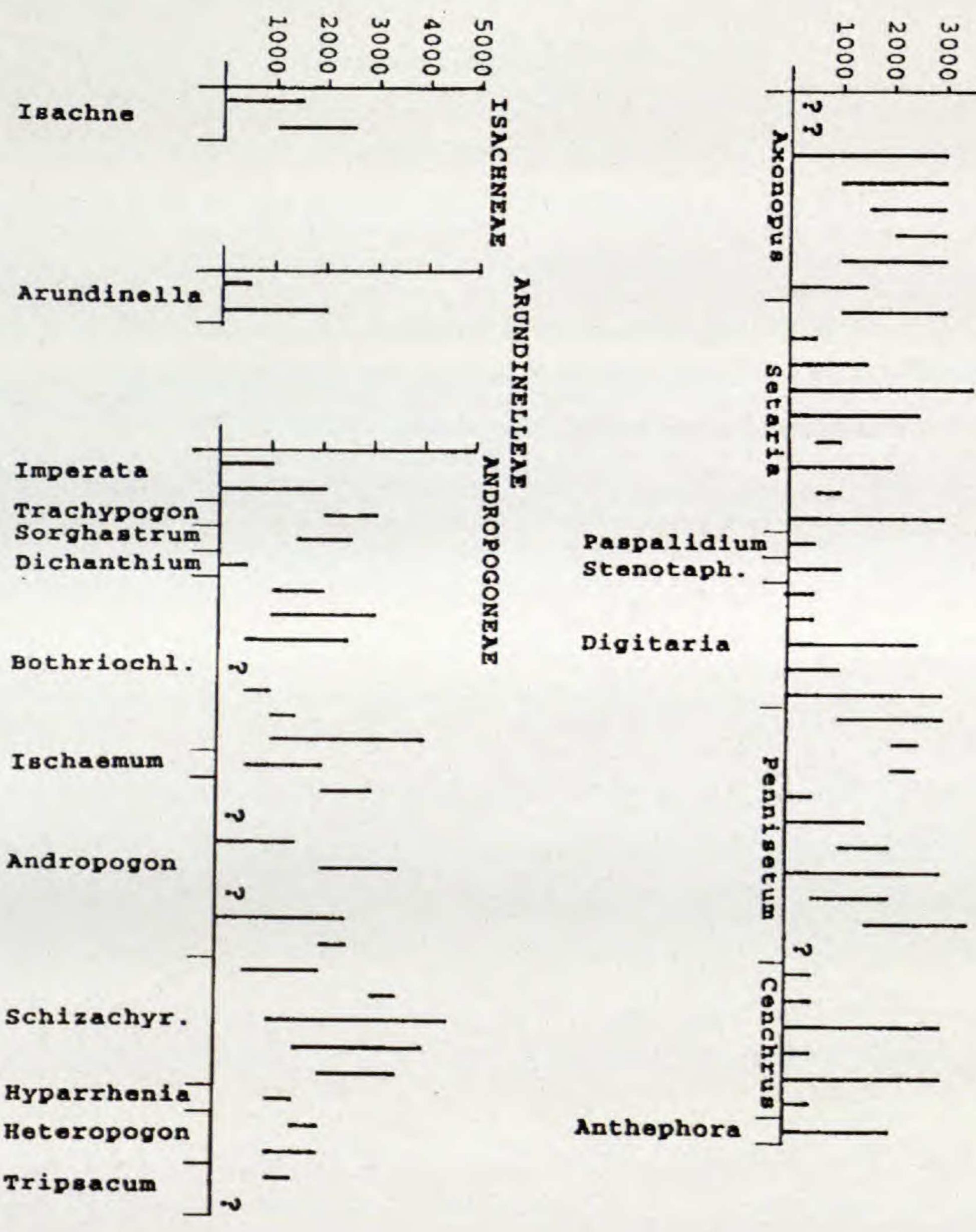

Figure 5. Altitudinal distribution of all native Ecuadorian Panicoideae (Paniceae p.p., Isachneae, Arundinellaeae, and Andropogoneae). Further explanation under Fig. 1.